

ARTHROPODS IN DECOMPOSING WOOD OF THE ATCHAFALAYA RIVER BASIN

B.G. LOCKABY *¹, B.D. KEELAND ², J.A. STANTURF ³,
M.D. RICE ¹, G. HODGES ⁴, AND R.M. GOVERNO ¹

ABSTRACT - Changes in arthropod populations (numbers of individuals identified to the family level in most cases) were studied during the decomposition of coarse woody debris (CWD) in the Atchafalaya River Basin of Louisiana. The arthropod study was linked with a CWD decomposition study installed after disturbance by Hurricane Andrew. Arthropod numbers were compared between two canopy disturbance classes and between two spatial orientations of CWD (i.e., suspended above- and in contact with the soil). Results during 30 months in the field suggested little influence of canopy disturbance or spatial orientation of CWD on arthropod numbers. Counts were most frequently dominated by Collembola and Acarina and peaked after 18-24 months within larger debris.

INTRODUCTION

Recognition of the important role of coarse woody debris (CWD) in several key functions and processes of forest ecosystems has grown considerably in recent years. Rarely included as a component in forest ecology research several decades ago, investigation of CWD occurs more frequently as perspectives slowly shift toward longer temporal scales in an effort to gain a more meaningful understanding of ecosystem integrity. As an example, CWD was often overlooked in many nutrient cycling studies because of its slow turnover relative to more labile forms of organic matter. However, recent recognition of its importance in longterm nutrient storage and release (in particular carbon) has stimulated increased interest (Harmon et al. 1986).

In addition to longterm nutrient dynamics, CWD plays a number of other critical roles. Apart from well documented functions in aquatic systems (Harmon et al. 1986), CWD may contribute to microhabitat availability for both terrestrial flora and fauna. In regard to habitat, the facilitative influence of CWD during vegetation succession in the northwestern US is well noted (Franklin and Hemstrom 1981). A similar but more subtle role in seedling recruitment has been suggested by Sharitz (1996) in wetland forests of the southeastern US. In the latter systems, the availability of slightly elevated microhabitat such as logs

* Corresponding author - lockabg@auburn.edu. ¹ School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL 36849. ² US Geologic Survey, Lafayette, LA 70506. ³ US Forest Service, Athens, GA, 30602. ⁴ Florida Department of Agriculture, Gainesville, FL 32601.

or stumps which is less subject to inundation may promote survival of some plant species.

Coarse woody debris is also important in regard to macro- and microfaunal habitat (Harmon et al. 1986). In particular, the importance of arthropod populations to ecosystem diversity has been reviewed by Carroll (1996) who outlined several issues and/or hypotheses which may be involved. According to Carroll, there are key questions related to system productivity, structure, and temporal stability which are pertinent to examinations of arthropod populations. Citing a lack of supporting evidence, Coleman et al. (1994) discount the notion of a direct linkage between soil community diversity and ecosystem stability.

There are indications of strong relationships between microbial populations and arthropods and these may be manifested through grazing pressures as well as other mechanisms (Couteaux and Bottner 1994). In addition, these authors note that arthropod influences on microbial communities vary depending on nutrient availability and that subsequent decomposition dynamics may be altered as a result of microbial community composition shifts in response to arthropod influences. Consequently, improved knowledge of taxonomic and functional changes in detrital populations can lead to a clearer understanding of nutrient cycling processes. Thus, our general objective is to determine whether relationships exist between numbers and taxonomy of arthropods and CWD decomposition following a major disturbance in a wetland forest. The occurrence of a major canopy disturbance and the resulting pulse of CWD inputs allowed examination of populations during decomposition under different environmental conditions as well.

Harmon et al. (1986) observed that, in spite of its obvious importance, CWD had often been ignored as a topic of study worldwide. Those authors felt that this was due, in part, to the length of time and difficulty in manipulation associated with its study. In reference to CWD in the south temperate forests of the US, McMinn and Crossley (1996) made the same observation regarding lack of research attention. In addition, there have been very few reports of CWD research in wetland forests in general (Harmon et al. 1986, Brown 1990). The latter statement is particularly true in regard to information on arthropod populations.

Due to the critical function of wetland forests in dissolved organic carbon export, descriptions of CWD dynamics in those systems are particularly needed. Based on calculations derived from US Forest Service volume estimates in mortality categories, McMinn and Hardt (1996) estimated CWD standing crops in lowland hardwood forests in Georgia and South Carolina to average 8.7 Mg/ha. These values

are similar to the range for fallen dead wood (i.e., 5.6–7.6 Mg/ha) measured in a bottomland hardwood forest of Illinois (Chueng and Brown 1995).

However, other estimates are higher. In the Great Dismal Swamp of Virginia, Day (1979) estimated dead wood biomass to range from 8.4 to 50.2 Mg/ha for four forest types there. Similarly, Schlesinger (1978) estimated 49 Mg/ha of snags and 2.7 Mg/ha of CWD in the Okefenokee Swamp of south Georgia. After hurricane disturbance in the Atchafalaya River Basin of Louisiana, Rice et al. (1997) estimated that approximately 66 and 125 Mg/ha of CWD existed on lightly and heavily disturbed portions respectively of the present study area. However, apart from a brief mention in Seastedt et al. (1989), we are unaware of any reports describing changes in arthropod populations during terrestrial decomposition in a wetland forest.

In generalized scenarios of successional changes in arthropod populations during CWD decomposition (Harmon et al. 1986), various Coleoptera are among the primary invaders of fresh CWD. An indirect effect of the initial invasion is the opening of secondary entry pathways for other organisms which may include representatives of Isoptera and Hymenoptera. Later, as decay has progressed to a fairly advanced stage, other Coleoptera, Diptera and, in particular, Collembola and Acarina become common. However, these authors stress that there may be considerable variation among successional sequences depending on the tree species involved as well as environmental conditions.

Given the information void that exists regarding arthropod assemblages in Southeastern floodplain forests, the general objective of the present study was to identify those groups that are present in CWD and examine how those vary as decay proceeds. In addition, the influence of a major canopy disturbance and size and position of CWD on those assemblages were points of interest.

METHODS

The site used was the Atchafalaya River Basin (ARB), an alluvial wetland in south Louisiana occupied by cypress-tupelo and mixed hardwood forest types. Based on N:P ratios in fresh detritus (Rice et al. 1997), the ARB would be classed as eutrophic according to the criteria suggested by Lockaby and Walbridge (1998). In 1992, Hurricane Andrew moved through the ARB causing variable levels of damage. Mixed hardwood forests were damaged to a greater extent than were cypress-tupelo forests (Doyle et al. 1995). Large amounts of CWD fell as a result of that damage and, consequently, a CWD decomposition study was installed in 1993 to track the fate of that material.

Six plots were delineated during the summer of 1993 in the mixed hardwood (i.e., northern) portion of the ARB with three plots being classed in each of the two disturbance categories: light and heavy canopy disturbance. Plots classed as light disturbance typically exhibited 70–75% canopy closure while heavily disturbed areas were much more open with only 25–30%. Given the tree species occurrence on those plots, a single species, pumpkin ash (*Fraxinus profunda* Bush.), was selected for use in the study. The study was restricted to one species in order to maintain sample numbers within reasonable limits. Woody material belonging to two diameter classes (fine woody debris (FWD - a pack of three twigs, 20 cm long by 0.5–2.5 cm in diameter) and large woody debris (LWD - single logs, 7.5–20.0 cm in diameter and 50 cm long) was collected and installed on plots. Twig packs (FWD) and single logs (LWD) were placed in two positions (i.e., suspended- 1 m above and in-contact with soil) to mimic realistic orientations following blowdowns. As an aid in interpretation of arthropod population differences, over the 30 month period, decomposition rate parameters (k) were 0.075, 0.050, 0.081, and 0.061 for LWD in heavy disturbance/contact position, heavy/suspended, light/contact, and light/suspended respectively. In the FWD category, parameters were 0.083, 0.054, 0.088, and 0.066 for the same respective designations (Rice et al. 1997).

FWD packs and LWD logs were retrieved from the field at 6 month intervals over a 30 month period beginning in October, 1993. Although this duration is brief compared to those of many CWD studies, the mass loss data and decay rates reported by Rice et al. (1997) indicate that CWD decomposition in this system is very rapid compared to that reported elsewhere. Thus, examination of arthropod populations across a shorter time frame is quite meaningful for the ARB and probably for south temperate riparian forests in general.

Since it was apparent that drying would have a profound effect on arthropod numbers, sample desiccation was prevented by placing samples in plastic bags upon collection. Extractions were performed on an entire pack basis for FWD and on a subsample basis for LWD. Field (fresh) weights were recorded on both packs and log subsamples and moisture content corrections were later applied so that dry weights could be calculated. Arthropod extractions were performed using a modified Berlese-Tullgren funnel (Seastedt and Crossley 1980). Extractions occurred over a five-day period during which packs and subsamples of logs were continuously exposed to light and heat. Arthropods separated in this manner were collected in 70% ethyl alcohol and stored. Later, arthropods were identified to the family level (in most cases) and counted.

Considerable temporal and spatial variation was encountered at the family level in terms of individual counts. Consequently, insufficient numbers existed to conduct statistical analyses at the family level in many cases. Thus, analyses were focused upon comparisons between disturbance classes, positions, and among collection dates at the ordinal level. ANOVAs were used to make these comparisons of arthropod numbers relativized to a wood mass basis. Counts are reported on a wood mass basis since quantities of CWD are usually expressed as per unit area: consequently, counts/100 g wood are readily comparable to amounts of CWD elsewhere. Statistical significance is reported at the $P > 10\%$ level as in Seastedt et al. (1989).

The study site, experimental design, and general approach used to examine mass and nutrient dynamics during decomposition of the same CWD materials used in the present study are described in detail in Rice et al. (1997).

RESULTS

Comparisons among disturbance classes for both LWD and FWD suggest no statistically significant trends in regard to disturbance effects (Tables 1 and 2). Arthropod populations within LWD at the 6 month collection were numerically dominated by Collembola, Thysanoptera, Acarina, and Coleoptera in that order regardless of disturbance class (Table 1). At 12 months and thereafter, Collembola and Acarina generally dominated although Thysanoptera were sometimes noteworthy as well (particularly at 18 months).

Table 1. Arthropod counts/100g wood found in large woody debris by disturbance category (L = low, H = high) in the Atchafalaya River Basin, LA.

Order	6 Months		12 Months		18 Months		24 Months		30 Months	
	L	H	L	H	L	H	L	H	L	H
Acarina	5.3	2.2*	2.1	5.6	17.1	9.6	2.2	5.4	10.4	10.2
Coleoptera	0.4	2.1	0.2	0.3	1.1	2.4	0.9	0.9	2.0	0.9
Collembola	21.6	5.0	10.3	19.8	29.6	11.8	17.1	92.5	25.1	23.0
Dermoptera	0.04	0.08*	-	-	-	-	-	-	0.14	0.26
Diptera	0.34	0.45	0.74	0.26	1.1	0.56	0.2	3.2	0.8	0.22*
Gastropoda	0.04	0.06	-	-	-	-	-	-	-	-
Hymenoptera	0.32	0.48	0.17	0.19	0.3	11.4	0.2	0.3	1.11	0.39
Psocoptera	0.04	0.37	-	-	0.2	0.2	-	-	-	-
Thysanoptera	6.2	4.6	-	-	156.0	0.5*	0.06	0.13*	6.1	0.13*
Crustacea	-	-	0.04	0.06	-	-	-	-	0.26	0.07
Hemiptera	-	-	0.07	0.06	0.24	0.20	-	-	0.22	0.08
Lepidoptera	-	-	0.06	0.06	-	-	0.2	0.3	-	-
Araneae	-	-	-	-	-	-	-	-	0.07	0.10
Chilopoda	-	-	-	-	-	-	-	-	1.8	0.18
Diplopoda	-	-	-	-	-	-	-	-	1.8	0.11
Isoptera	-	-	-	-	-	-	-	-	0.17	0.25

* Significant difference between disturbance types within the same collection period.

Compared to CWD, fewer Orders were represented in the FWD category although those Orders present were generally represented by higher counts (Table 2). Psocoptera were most numerous at the initial collection. However, Acarina and Collembola made their appearance (at least to the degree to which statistical analysis was possible) at the 12 and 18 month collections respectively and exhibited fairly high counts. In addition, Coleoptera were numerous as well in the same collections. Later, Diptera also became quite important and, at the 30 month collection, ranked second only to Collembola. Thus, for both FWD and CWD, Collembola were most numerous in the advanced stages of decomposition.

As in the case of disturbance regime comparisons, no statistically significant trends were evident in comparisons of positions for LWD (Table 3). When averaged across disturbance regimes as in Table 3, there were clearly many more Orders represented at 30 months than were seen previously. However, FWD counts suggested a tendency

Table 2. Arthropod counts/100g wood found in fine woody debris by disturbance category (L = low, H = high) in the Atchafalaya River Basin, LA.

Order	6 Months		12 Months		18 Months		24 Months		30 Months	
	L	H	L	H	L	H	L	H	L	H
Coleoptera	6.2	4.6	4.8	9.5	8.0	6.0	7.0	5.0	-	-
Diptera	5.0	3.7	4.4	11.1*	-	-	12.6	7.3	7.11	4.3
Psocoptera	3.8	21.3	4.6	4.6	-	-	-	-	-	-
Acarina	-	-	7.6	11.0	4.0	4.0	18.0	9.0	0.13	0.37
Collembola	-	-	-	-	16.2	7.6	-	-	34.5	9.2

* Significant difference between disturbance types within the same collection period.

Table 3. Arthropod counts/100g wood found in large woody debris by position (C = contact with soil, S = suspended) in the Atchafalaya River Basin, LA.

Order	6 Months		12 Months		18 Months		24 Months		30 Months	
	C	S	C	S	C	S	C	S	C	S
Acarina	3.6	3.5	4.7	4.5	17.7	7.5	6.0	2.6	10.8	9.9
Coleoptera	2.1	0.5	0.28	0.19	1.5	2.2	1.1	0.14	1.4	1.3
Collembola	21.1	2.2	0.16	0.14	32.5	5.3*	114.1	13.5	11.7	34.1*
Dermoptera	0.04	0.08*	-	-	-	-	-	-	0.22	0.16
Diptera	0.50	0.25	0.67	0.23	-	-	3.3	0.14	0.54	0.48
Hymenoptera	0.6	0.18	0.18	0.18	13.1	0.9	0.30	0.14	0.60	0.80
Psocoptera	0.21	0.16	-	-	-	-	-	-	-	-
Hemiptera	-	-	0.06	0.07	0.23	0.19	-	-	-	-
Lepidoptera	-	-	0.05	0.07*	-	-	0.18	0.29	0.22	0.15
Thysanoptera	-	-	-	-	-	-	0.06	0.14*	0.06	2.1
Chilopoda	-	-	-	-	-	-	-	-	0.26	0.95
Crustacea	-	-	-	-	-	-	-	-	0.41	0.09
Diplopoda	-	-	-	-	-	-	-	-	1.4	0.10
Isoptera	-	-	-	-	-	-	-	-	0.38	0.16
Neuroptera	-	-	-	-	-	-	-	-	0.15	0.12

* Significant difference between positions within the same collection period.

toward higher numbers in FWD in contact with soil in some cases (Table 4). As examples, Diptera at 12 and 30 months, as well as Acarina and Psocoptera at 24 months displayed this tendency.

Comparison of LWD counts across time indicated that numbers within Orders (where temporal statistical differences could be demonstrated) maximized near 18 to 24 months (Table 5, Fig. 1). This was true for Acarina, Coleoptera, Collembola, and Diptera. Lepidoptera was an exception having peaked at the first (6 month) collection. In addition, counts of several other Orders, which did not show statistically significant temporal variation, exhibited maximum counts near 18–24 months. The latter group included Araneae, Hemiptera, Psocoptera, and Thysanoptera.

As previously indicated, temporal trends in FWD counts were examined separately by position since there were indications of a position effect on counts in the cases of several orders (Figs. 2 and 3). However, in neither the FWD-contact (Fig. 2) nor FWD-suspended (Fig. 3) did total counts follow the temporal trend (i.e., maximization

Table 4. Arthropod counts/100g wood found in fine woody debris by position (C = contact with soil, S = suspended) in the Atchafalaya River Basin, LA.

Order	6 Months		12 Months		18 Months		24 Months		30 Months	
	C	S	C	S	C	S	C	S	C	S
Coleoptera	4.9	5.5	9.8	4.2	3.9	10.1	4.9	7.0	-	-
Diptera	4.7	4.2	12.3	3.8*	-	-	7.3	12.6	9.1	4.7*
Psocoptera	3.7	39.1*	4.9	4.3*	-	-	4.9	3.7*	-	-
Acarina	-	-	11.5	7.2	3.9	4.1	18.5	3.7*	-	-
Collembola	-	-	-	-	16.2	12.0	-	-	5.5	38.2

* Significant difference between positions within the same collection period.

Table 5. Arthropod counts/100g wood in large woody debris (means followed by same letter within rows are not significantly different).

Order	6 Months	12 Months	18 Months	24 Months	30 Months
Acarina	3.6 B	4.1 B	12.6 A	4.5 B	10.3 A B
Araneae	0.08	0.07	0.15	-	0.10
Chilopoda	0.05	0.05	3.7	-	0.72
Coleoptera	1.3 A B	0.25 B	1.9 A	0.9 A B	1.4 A B
Collembola	12.5 A	15.1 A	18.9 A	71.0 B	23.9 A
Crustacea	0.18	0.05	0.08	0.20	0.22
Dermaptera	0.05	0.14	0.09	-	0.17
Diplopoda	0.52	-	-	-	1.0
Diptera	0.41 A	0.47 A	0.80 A	2.6 B	0.51 A
Gastropoda	0.05	-	0.07	0.18	0.26
Hemiptera	0.18	0.06	0.20	-	0.13
Homoptera	-	0.04	0.17	-	0.17
Hymenoptera	0.41	0.18	7.0	0.27	0.70
Isoptera	0.29	-	-	-	0.23
Lepidoptera	0.43 A	0.06 B	0.12 B C	0.25 C	0.20 B C
Psocoptera	0.20	0.07	0.21	0.31	0.05
Thysanoptera	0.10	0	52.4	0.10	1.6

near 18–24 months) observed with LWD. Although count maximization for particular orders near the 18–24 month collections were apparent in some cases (e.g., Acarina - Contact, Diptera - suspended), there was less evidence of distinct time periods where maxima or minima occurred (Table 6). Although temporal variation in FWD

Table 6. Arthropod counts/100g wood in fine woody debris in two positions (means followed by same letter within rows are not significantly different).

Order	6 Months	12 Months	18 Months	24 Months	30 Months
Acarina	3.6 A	11.5 A B	3.9 A	18.5 B	12.7 B
Coleoptera	4.9	9.8	3.9	4.9	6.1
Collembola	23.1	9.9	16.2	4.9	5.5
Diptera	4.7 A	12.4 B	3.8 A	7.3 A B	9.1 A B
Hymenoptera	10.8 A	5.0 B	-	-	-
Lepidoptera	5.8	-	-	5.2	12.1
Psocoptera	3.7 A	4.9 B	-	4.9 B	6.1 C
Suspended					
Acarina	5.5	4.2	10.2	7.0	-
Collembola	-	4.2	12.0	16.7	38.2
Diptera	4.2 A	5.8 A	4.2 A	12.6 B	4.7 A
Psocoptera	39.1 A	4.3 B	16.6 C	3.7 D	-
Thysanoptera	-	4.2	4.1	-	4.7

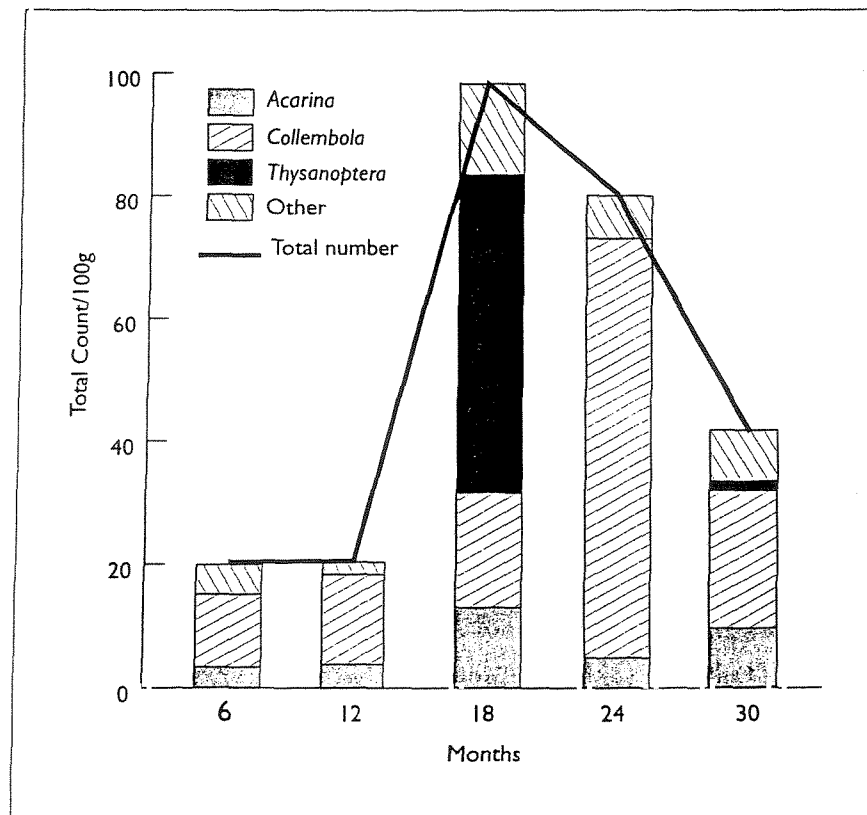


Figure 1. Major groups (number/100g wood) in large woody debris.

counts was often statistically significant, the nature of that variation was highly Order- specific.

Although statistical analyses were not conducted at the family level for reasons already discussed, Table 7 provides a general list of those families which were extracted over the course of the study.

DISCUSSION

The numerical dominance of Collembola in LWD and generally in FWD does not correspond to results from CWD studies on upland sites in Montana and riparian sites in Kansas (Seastedt et al. 1989). Those authors found Acarina to be most abundant by a large margin. Similarly, Abbott and Crossley (1982) found Acarina and Collembola were the most numerous orders in CWD of a southern Appalachian site. Acarina

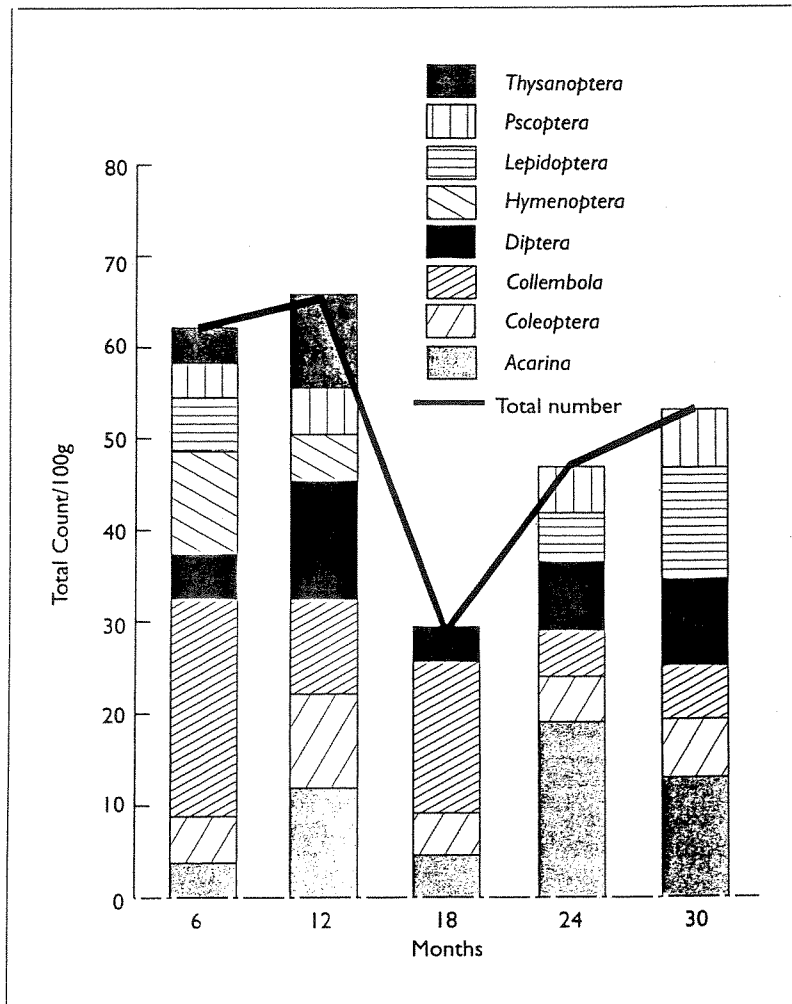


Figure 2. Major groups (number/100g wood) in fine woody debris in contact with soil.

might be expected to occur most frequently since that order represents the most abundant arthropod group in nature (Coleman and Crossley 1996). In the present study, Acarina did dominate in some of the later samplings of FWD.

The higher abundances per 100 g of wood recorded on FWD compared to LWD are reasonable. Abbott and Crossley (1982) also noted higher counts on twigs compared to logs. This differential is probably primarily due to larger surface areas per unit mass in the smaller diameter material. Secondary reasons may include nutritional differences which may have stimulated variation between FWD and LWD in terms of microflora. However, the more spacious habitat available in LWD apparently attracted representatives of many more orders than were recorded in FWD.

Disturbance regime had little effect on arthropod counts since the extent of canopy disturbance apparently had minimal influence on CWD

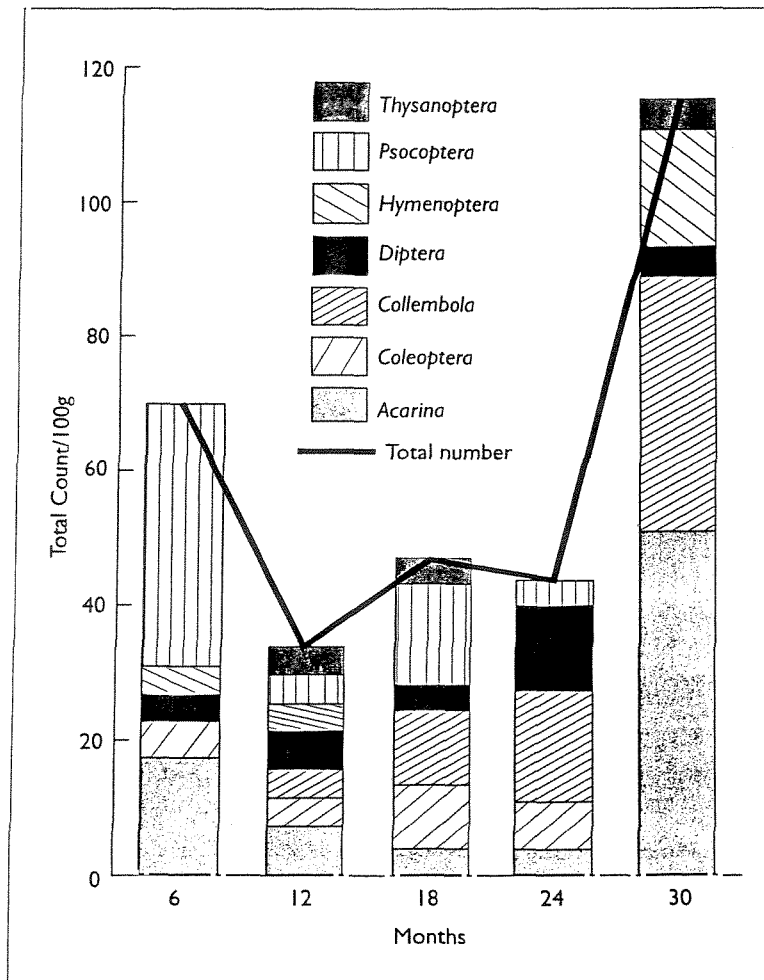


Figure 3. Major groups (number/100g wood) in fine woody debris suspended above the soil surface.

decomposition in general (Rice et al. 1997). However, decomposition dynamics were strongly influenced by position (Rice et al. 1997) and, consequently, the lack of a similar influence on counts in LWD was surprising. Intuitively, it might be expected that CWD in contact with soil would have much greater opportunities afforded for arthropod invasion. Also, the lack of an obvious relation between LWD counts and position suggests that there is not a strong relationship between extent of decay at a given point in time vs. arthropod abundance in the ARB.

In the present study, reasons for the tendency of LWD counts to peak near the 18 and/or 24 month collections are unclear. Other investigations of arthropod abundance vs. time that CWD had been in the field have produced mixed results. Some investigators have not found a strong relationship between extent of decomposition and abundance of arthropods (Seastedt et al. 1989). However, Abbott and Crossley (1982) observed that numbers generally increased with time in the field. In addition, the relationships described between season and mite abundance (Coleman and Crossley 1996) suggest that the particular season when a collection date was made did not influence counts. Rather, the frequent occurrence among Orders of a 18–24 month peak may suggest a successional tendency during LWD breakdown in systems such as the ARB. In all cases, decay for both LWD and FWD followed a negative exponential pattern so that any relationship between arthropod counts and percent mass remaining was not apparent.

Temporal variation for FWD counts in terms of maxima and minima are almost inversely related to those described for LWD. The lack of synchronicity between L- and FWD counts suggests that a single abiotic influence such as hydroperiod is unlikely to have caused both patterns. Comparing 1993–96 monthly stage levels at Butte La Rose in the northern end of the ARB (personal communication - US Army Corps of Engineers - Baton Rouge, LA) with L- and FWD counts does not suggest a linkage with peak stages (i.e., periods when sites were possibly inundated). Thus, the occurrence of maximum arthropod populations does not seem to be a direct response to recent flood events.

Contrasting tendencies toward immobilization for nitrogen vs. mineralization for phosphorus in CWD (Rice et al. 1997) suggest that microbial processes in the ARB are likely nitrogen-limited. Although highly speculative, there may be some relation between the occurrence of peak nitrogen content in the LWD at 12 months (Rice et al. 1997) and subsequent counts at 18–24 months if arthropod communities were responding to grazing opportunities derived from the expanded microbial biomass associated with nitrogen immobilization. This type of response might be similar in nature to that observed for a Collembolan whose growth and fecundity increased upon exposure to fungi from a high-nitrogen environment (Booth and Anderson 1979 as cited in

Couteaux and Bottner 1994). However, investigation of possible linkages between nitrogen dynamics and arthropod succession in the ARB may be appropriate for later study.

LITERATURE CITED

- ABBOTT, D.T., and D.A. CROSSLEY. 1982. Woody litter decomposition following clear-cutting. *Ecology* 63:35–42.
- BOOTH, R.G., and J.M. ANDERSON. 1979. The influence of fungal food quality on the growth and fecundity of *Folsomia candida* (Collembola: Isotomidae). *Oecologia* 38:317–323.
- BROWN, S. 1990. Structure and dynamics of basin forested wetlands in North America. Pp. 171–199, *In* A. Lugo, M. Brinson, and S. Brown (Eds.). *Ecosystems of the World 15: Forested Wetlands*. Elsevier, NY. 527 pp.
- CARROLL, C.R. 1996. Coarse woody debris in forest ecosystems: an overview of biodiversity issues and concepts. Pp. 25–28, *In* J.W. McMin, and D.A. Crossley (Eds.). *Biodiversity and Coarse Woody Debris in Southern Forests*. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service General Technical Report SE-94. Southern Research Station, Asheville, NC.
- CHUENG, N., and S. BROWN. 1995. Decomposition of silver maple (*Acer saccharinum* L.) woody debris in a central Illinois bottomland forest. *Wetlands* 15:232–241.
- COLEMAN, D.C. and D.A. CROSSLEY. 1996. *Fundamentals of soil ecology*. Academic Press, NY. 205 pp.
- COLEMAN, D.C., J. DIGHTON, K. RITZ, and K.E. GILLER. 1994. Perspectives on the compositional and functional analysis of soil communities. Pp. 261–271, *In* K. Ritz, J. Dighton, and K.E. Giller (Eds.). *Beyond the Biomass*. British Society of Soil Science.
- COUTEAUX, M.M., and P. BOTTNER. 1994. Biological interactions between fauna and the microbial community in soils. Pp. 159–172, *In* K. Ritz, J. Dighton, and K.E. Giller (Eds.). *Beyond the Biomass*. British Society of Soil Science.
- DAY, F.P. 1979. Litter accumulation in four plant communities in the Great Dismal Swamp. *American Midland Naturalist* 102:281–289.
- DOYLE, T.W., B.D. KEELAND, L.E. GORHAM, and D.J. JOHNSON. 1995. Structural impact of Hurricane Andrew on the forested wetlands of the Atchafalaya River Basin in south Louisiana. *Journal Coastal Research* 21:354–364.
- FRANKLIN, J.F., and M.A. HEMSTROM. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Pp. 212–229, *In* D.C. West, H.H. Shugart, and D.B. Botkin (Eds.). *Forest succession: concepts and application*. Springer-Verlag, NY. 517 pp.
- HARMON, M.E., J.F. FRANKLIN, F.J. SWANSON, P. SOLLINS, S.V. GREGORY, J.D. LATTIN, N.H. ANDERSON, S.P. CLINE, N.G. AUMEN, J.R. SEDELL, G.W. LIENKAEMPER, K. CROMACK, and K.W. CUMMINS. 1986. Ecology of coarse woody debris in temperate ecosystems. Pp. 133–302, *In* A. MacFayden and E.D. Ford (Eds.). *Advances in Ecological Research* Vol. 15. Academic Press. London.

- LOCKABY, B.G., and M.R. WALBRIDGE. 1998. Biogeochemistry. Pp. 149–172, In W. Conner, and M. Messina (Eds.). *Southern Forested Wetlands Ecology and Management*. Lewis Publishers, Boca Raton, FL. 616 pp.
- McMINN, J.W., and D.A. CROSSLEY, Jr. 1996. Preface. Pp. iii, In J.W. McMinn, and D.A. Crossley (Eds.). *Biodiversity and Coarse Woody Debris in Southern Forests*. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service General Technical Report SE-94. Southern Research Station, Asheville, NC.
- McMINN, J.W., and R.A. HARDT. 1996. Accumulations of coarse woody debris in southern forests. Pp. 1–9, In J.W. McMinn, and D.A. Crossley (Eds.). *Biodiversity and Coarse Woody Debris in Southern Forests*. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service General Technical Report SE-94. Southern Research Station, Asheville, NC.
- RICE, M.D., B.G. LOCKABY, J.A. STANTURF, and B.D. KEELAND. 1997. Woody debris decomposition in the Atchafalaya River Basin of Louisiana following hurricane disturbance. *Soil Science Society of America Journal* 61:1264–1274.
- SCHLESINGER, W.H. 1978. Community structure, dynamics, and nutrient ecology in the Okefenokee cypress swamp-forest. *Ecological Monographs* 48:43–65.
- SEASTEDT, T.R., and D.A. CROSSLEY. 1980. Effects of arthropods on the seasonal dynamics of nutrients in forest litter. *Soil Biology and Biochemistry* 12:337–342.
- SEASTEDT, T.R., V.M. REDDY, and S.P. CLINE. 1989. Arthropods in decaying wood from temperate coniferous forests. *Pedobiologia* 33:69–77.
- SHARITZ, R.R. 1996. Coarse woody debris and woody seedling recruitment in southeastern forests. Pp. 29–34, In J.W. McMinn, and D.A. Crossley (Eds.). *Biodiversity and Coarse Woody Debris in Southern Forests*. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Forest Service General Technical Report SE-94. Southern Research Station, Asheville, NC.